Impact of rainbow smelt (*Osmerus mordax*) invasion on walleye (*Sander vitreus*) recruitment in Wisconsin lakes

Norman Mercado-Silva, Greg G. Sass, Brian M. Roth, Stephen Gilbert, and M. Jake Vander Zanden

Abstract: Rainbow smelt (*Osmerus mordax*) are invaders of inland lakes in the Laurentian Great Lakes region of North America and have negatively affected native fish populations. Walleye (*Sander vitreus*) comprise an important fishery throughout the Great Lakes region and could be affected by rainbow smelt invasions. We test for declines of young-of-the-year walleye (YOY-W) density in 12 of the 26 known rainbow smelt invaded lakes in Wisconsin. Invaded lakes showed significantly lower YOY-W densities than uninvaded lakes during the period 1985–2004. In 94% (17/18) of years, YOY-W densities from invaded lakes were lower than those from uninvaded lakes. Declines (~70%) in YOY-W densities were observed in three lakes with data from before and after rainbow smelt invasion. For 10 invaded lakes with more than two YOY-W density estimates between 1985 and 2004, YOY-W densities averaged 13% below expected densities. Our results demonstrate the potential impacts of rainbow smelt invasion on walleye tribal, commercial, and recreational fisheries and highlight the importance of preventing their further spread.

Résumé : Les éperlans arc-en-ciel (*Osmerus mordax*) sont des envahisseurs des lacs intérieurs de la région des Grands Lacs laurentiens d'Amérique du Nord et ils ont affecté négativement les populations de poissons indigènes. Le doré (*Sander vitreus*) est une espèce importante pour la pêche dans toute la région des Grands Lacs et il peut être affecté par les invasions d'éperlans arc-en-ciel. Nous vérifions les déclins de jeunes dorés de l'année (YOY-W) dans 12 des 26 lacs du Wisconsin qui ont connu une invasion d'éperlans arc-en-ciel. Les lacs envahis possèdent des densités de YOY-W significativement plus faibles que les lacs non envahis durant la période 1985–2004. Dans 94 % (17/18) des années, les densités des YOY-W dans les lacs envahis sont plus faibles que celles des lacs non envahis. Dans trois lacs pour lesquels il existe des données avant et après l'invasion des éperlans arc-en-ciel, il s'est produit un déclin (~70 %) des densités des YOY-W. Dans 10 lacs pour lesquels il y a plus de deux estimations de la densité des YOY-W entre 1985 et 2004, les densités de YOY-W sont en moyenne 13 % inférieures aux densités attendues. Nos résultats démontrent les impacts potentiels des invasions des éperlans arc-en-ciel sur les pêches tribales, commerciales et sportives de dorés; ils soulignent l'importance d'enrayer l'expansion des invasions.

[Traduit par la Rédaction]

Introduction

Invasive species are a major threat to freshwater ecosystems (Sala et al. 2000; Vander Zanden 2005) and can have significant impacts on valuable fisheries via habitat alteration, predation, and competitive interactions (Moyle et al. 1987; Madenjian et al. 2002; Sullivan et al. 2003). Exotic fishes alone cause over US$1 billion annually in economic losses, even when many species are intentionally introduced to enhance fisheries (Pimentel et al. 2000, 2001). Identifying invasive species impacts and forecasting the spread of invaders are currently areas of intense research (Lodge 1993; Lodge et al. 1998; Vander Zanden et al. 2004). Impacts of invasive species sometimes involve easily observable responses from the recipient ecosystems, though effects often are difficult to elucidate because they affect ecological processes with high natural variation, such as recruitment.

Rainbow smelt (*Osmerus mordax*) are incipient invaders in inland lakes of the Great Lakes region (Evans and Loftus 1987; Hrabik and Magnuson 1999; Mercado-Silva et al.

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2006), and their introduction has led to the extirpation of native fishes (e.g., yellow perch, *Perca flavescens*, and cisco, *Coregonus artedi*) via competitive or predatory interactions (Evans and Waring 1987; Hrabik et al. 1998, 2001). Rainbow smelt are also suspected to affect walleye (*Sander vitreus*) (Schneider and Leach 1977; Johnson and Goettl 1999), which comprise an important fishery in the Great Lakes region (Schneider and Leach 1977; Becker 1983; Bureau of Indian Affairs (BIA) 2003). Current hypotheses are that rainbow smelt cause recruitment failure through either competitive or predatory interactions with young-of-the-year walleye (YOY-W) (Schneider and Leach 1977; Johnson and Goettl 1999). However, direct evidence is lacking because walleye recruitment is highly variable among years and lakes (Hansen et al. 1998; Beard et al. 2003; Sass et al. 2004), rainbow smelt have invaded relatively few lakes, and their impact on any given lake may be variable. In addition, rainbow smelt effects may occur rapidly, thereby preventing an adequate field investigation of potential causal mechanisms. Regardless of these limitations, it is imperative to document evidence of impact early in the invasion process to better understand the possible consequences of further rainbow smelt expansion.

Here, we examine empirical evidence for the effect of rainbow smelt invasions on walleye recruitment in Wisconsin lakes by comparing YOY-W densities among invaded and uninvaded lakes and studying recruitment trends in invaded lakes. We expect that densities of YOY-W will be lower in rainbow smelt invaded lakes relative to uninvaded lakes and that declines in YOY-W densities will be observed in invaded lakes. To our knowledge, this is the first study that investigates rainbow smelt effects on walleye recruitment through time and among lakes by making use of data from before and after rainbow smelt invasion, producing information important for the future management of walleye populations and the prevention of rainbow smelt expansion.

Materials and methods

Study region

In the northern third of Wisconsin (US) (i.e., ceded territory), 859 inland lakes are known to contain naturally reproducing and stocked walleye populations (Nate et al. 2000; Sass et al. 2004). Among-year variability in recruitment of young-of-the-year (age-0) walleye (YOY-W) to the adult population is driven by parental stock size, predation, competition, water temperatures, changes in spawning habitat, and interannual climate variability (Hansen et al. 1998; Nate et al. 2000; Beard et al. 2003), though other anthropogenic factors may also play an important role. Fishery pressure and habitat degradation also affect the viability of Wisconsin walleye populations (BIA 2003) and, ultimately, walleye recruitment. Walleye recruitment declines have been linked to rainbow smelt introductions in some systems in the US, presumably because of direct larval and egg predation by rainbow smelt or through food web disruptions (Schneider and Leach 1977; Jones et al. 1994; Roth 2005).

Rainbow smelt became established in Lake Michigan and Lake Superior in the 1920s and 1930s and then spread to inland lakes in the Great Lakes, Mississippi, and Hudson Bay watersheds (Evans and Loftus 1987; Franzin et al. 1994; Mercado-Silva et al. 2006). By 1968, several inland Wisconsin lakes (especially deep, cold-water, oligotrophic lakes) had established rainbow smelt populations (Becker 1983).

Data

We obtained YOY-W density estimates from the Wisconsin Department of Natural Resources (WDNR) and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) databases. Systematic lake surveys started in 1990 and have continued to date but were preceded by monitoring efforts starting as early as 1958 in a limited number of lakes. YOY-W density was estimated by electrofishing the entire lake shoreline with electrofishing (230V AC) boats from mid-September to mid-October of each year on lakes selected under a randomized survey design. If the entire shoreline could not be sampled, randomly selected sections were subsampled (in 946 of 3182 samples) and the distance sampled was recorded. The number of lakes surveyed varied among years (minimum, 25 in 1985 and 2004; maximum, 273 in 2002), and most lakes were not sampled in consecutive years. Age-0 fish were identified by examining the length frequency distribution for modal lengths or through annuli analysis (Beard et al. 2003). Densities were calculated as the number of YOY-W captured divided by the shoreline length (kilometres) sampled (Serns 1982, 1983). For our analysis, we used data from 432 walleye populations surveyed between 1971 and 2004. Most estimates were from the period 1985–2004. The data set had a high proportion of zero, or close-to-zero, YOY-W density estimates. Lakes used in our analysis ranged from 8 ha to 6200 ha in surface area. Lakes from which no YOY-W were collected in the entire data set were not used for analysis.

Rainbow smelt distribution in Wisconsin lakes was summarized from published literature (Becker 1983; Colby et al. 1987; McLain 1991; Hrabik and Magnuson 1999; Lyons et al. 2000; Krueger and Hrabik 2005), interviews with WDNR regional fish managers (see Acknowledgements), and data sets in the Wisconsin Aquatic Gap Mapping Application (WDNR) (http://web2.er.usgs.gov/wdnrfish/). Currently, 26 inland Wisconsin lakes are known to support rainbow smelt (Table 1). Twelve of these invaded lakes have been surveyed for YOY-W density, and three have YOY-W data from before and after rainbow smelt invasion. Long-term rainbow smelt abundance data are available for Sparkling Lake, Vilas County, from sampling carried out through the North Temperate Lakes – Long Term Ecological Research (NTL–LTER) program (http://limnology.wisc.edu/) and the WDNR. Rainbow smelt abundance was estimated as the number of rainbow smelt per fyke net from field samplings carried out yearly in early spring from 1981–2003.

Analysis

We conducted three separate analyses to test for rainbow smelt impact on walleye recruitment. First, we compared mean YOY-W densities (YOY-W$\cdot$km^{-1}) from lakes with (n = 12) and without (n = 420) rainbow smelt and between lakes where walleye recruitment is the product of natural reproduction (n = 133) and those lakes that are stocked (n = 287) (Mann–Whitney tests at α = 0.05 significance) using all available data from 1985–2004.

Table 1. Known rainbow smelt (*Osmerus mordax*) invaded inland lakes in Wisconsin.

Lake	County	Invasion year	Maximum depth (m)	Surface area (ha)	YOY-W data	Years sampled	Latitude (°N)	Longitude (°W)
1. Anderson	Vilas	1980s	19	13		0	46.17	–89.34
2. Beaver Dam	Barron	1980	32	450	×	7	45.53	–92.02
3. Big Cedar	Washington	1985	32	377		0	43.38	–88.25
4. Cisco	Bayfield	1983	32	38	×	2	46.37	–91.25
5. Crawling Stone	Vilas	1975	26	593		0	45.94	–89.89
6. Crystal	Vilas	1980s	20	35		0	46.10	–89.87
7. Dead Pike	Vilas	1990	24	120	×	5	46.06	–89.90
8. Diamond	Bayfield	NA	25	138	×	9	46.26	–91.14
9. Fence	Vilas	1968	26	1438	×	1	45.96	–89.95
10. Flambeau	Vilas	NA	26	476		0	45.96	–89.92
11. Keyes	Florence	1990	23	82	×*	13	45.90	–88.30
12. Little Crawling Stone	Vilas	NA	13	43		0	45.93	–89.90
13. Little Trout	Vilas	NA	29	395		0	46.08	–89.96
14. Little Bass	Vilas	1967	6.5	14		0	46.06	–89.17
15. Long Interlaken	Vilas	NA	20	149		0	46.07	–89.02
16. Long	Vilas	1985	29	352	×*	12	46.07	–89.17
17. Lucerne	Forest	1965	22	415	×	20	45.52	–88.85
18. Moss	Vilas	NA	8	79		0	45.96	–89.89
19. Placid Twin (N)	Vilas	NA	7	13		0	45.92	–89.83
20. Pokegama	Vilas	NA	19	425	×	1	45.99	–89.88
21. Sand Bar	Bayfield	1962	15	47		0	46.37	–91.53
22. Sparkling	Vilas	1981	20	51	×*	20	46.01	–89.70
23. To-To-Tom	Vilas	NA				0	45.96	–89.91
24. Tomahawk	Bayfield	NA	13	54		0	46.37	–91.52
25. Whitefish	Sawyer	1977	32	318	×	9	45.86	–91.45
26. Whitefish (Bardon)	Douglas	NA	31	336	×	13	46.20	–91.88

Note: Approximate or known detection year for rainbow smelt in each individual lake is indicated. Young-of-the-year walleye (YOY-W) data for analysis was available (pre- and post-invasion (×*) or postinvasion only (×)) for some of these lakes. "Years sampled" refers to the number of years that density of YOY-W was estimated for a given inland lake. The presence of rainbow smelt in Emily Lake (Florence County) has been suggested but not confirmed.

Second, we tested whether invaded lakes had lower YOY-W densities than uninvaded lakes within a given year between 1986 and 2003. Mean YOY-W densities from uninvaded and invaded lakes were compared for each year in this period. We omitted 1985 and 2004 from this analysis because we lacked sufficient data from invaded lakes. For each year, we conducted Mann–Whitney tests comparing YOY-W densities from invaded and uninvaded lakes (with significance at $\alpha = 0.05$), expecting lower densities in invaded lakes compared with uninvaded lakes. Further, we standardized the difference between mean densities from uninvaded and invaded lakes by dividing the difference by the standard deviation of the YOY-W densities from uninvaded lakes. Thus, the natural variability observed in uninvaded lakes was considered in establishing the effect from rainbow smelt invasion. We then calculated the percentage of years in the 1986–2003 period in which the mean YOY-W density from invaded lakes fell below the standardized mean from uninvaded lakes.

Third, we examined YOY-W densities from pre- and post-invasion periods in three invaded lakes (Sparkling, Vilas County; Long, Vilas County; Keyes, Florence County). All three walleye populations were supported by natural recruitment until the mid-1980s, mid-1990s, and early 2000s, respectively, when stocking of fingerling (~70 mm total length) and extended-growth (>120 mm total length) walleye was initiated by the WDNR. Estimates of YOY-W densities were available from these lakes for periods close to (Long) or before and after (Sparkling and Keyes) rainbow smelt were first observed. For each lake, we compared mean YOY-W densities among pre-invasion and five 5-year post-invasion periods. We calculated change in percentile terms by averaging YOY-W densities from all five postinvasion periods and comparing this value with the value from the pre-invasion or close to invasion period. Pre- and post-invasion periods were established with reference to the first reported observation of rainbow smelt in each lake.

Lake-specific differences

In addition to comparisons of YOY-W densities between invaded and uninvaded lakes, we examined whether rainbow smelt effect on walleye recruitment varied as a function of lake attributes. To do this, we calculated mean YOY-W density for each year for uninvaded lakes for the period 1985–2004. Next, we calculated the deviation of the YOY-W density in each invaded lake from the above mean for each year. We included only invaded lakes with more than 2 years of postinvasion data. The mean deviation was calculated for each lake and was expressed as the percent deviation from mean age-0-W density for uninvaded lakes. We tested whether this lake-specific measure of recruitment impact was correlated to morphometric and physiochemical variables by regressing it on lake area, maximum depth, mean Secchi depth, and pH (independent variables).

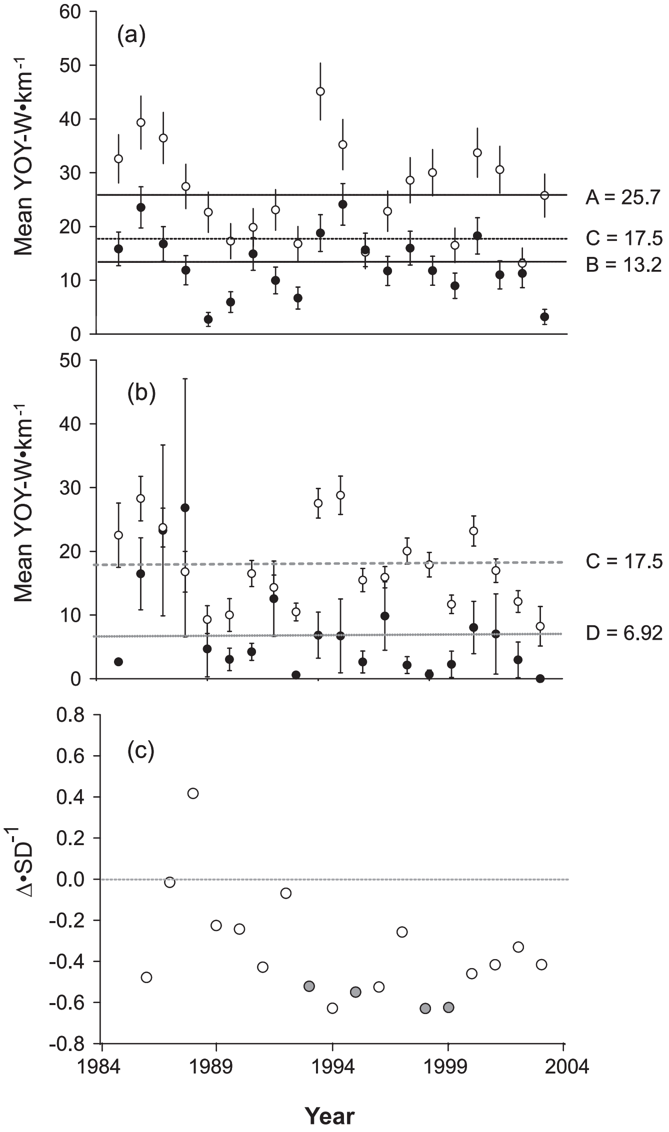
Results

YOY-W densities were lower in invaded than in uninvaded lakes across years. Densities of YOY-W were variable among years and lakes and showed no overall trend between 1985 and 2004 (Fig. 1*a*). Mean YOY-W density for uninvaded lakes was 17.5 YOY-W·(km of shoreline)$^{-1}$. Lakes with natural recruitment averaged 25.7 YOY-W·(km of shoreline)$^{-1}$ (range, 0.07 to 74.9; maximum YOY-W density in a lake, 263), and stocked lakes averaged 13.2 YOY-W·(km of shoreline)$^{-1}$ (range, 0.026 to 119.3; maximum YOY-W density in a lake, 283). YOY-W densities were significantly lower in stocked (n = 1981) lakes compared with lakes with natural recruitment (n = 1059) (χ^2 approximation of Mann–Whitney's U = 270, df = 1, $p < 0.001$) (Fig. 1*a*). Rainbow smelt invaded lakes had an average 6.92 YOY-W·(km of shoreline)$^{-1}$ (range, 0.1 to 46.6; maximum YOY-W density in a lake, 87). Invaded lakes had significantly lower YOY-W density than uninvaded lakes (χ^2 = 27.79, df = 1, $p < 0.001$; n invaded = 100, n uninvaded = 3040).

Rainbow smelt generally had a negative effect on walleye recruitment. In 17 of 18 (94%) years in the 1986–2003 period, invaded lakes had lower recruitment than uninvaded lakes (Figs. 1*b*, 1*c*). This difference was statistically significant ($p < 0.05$) in four years: 1993 (χ^2 = 3.92, df = 1, p = 0.048 [n invaded = 5, n uninvaded = 188]), 1995 (χ^2 = 4.18, df = 1, p = 0.041 [5, 178]), 1998 (χ^2 = 6.06, df = 1, p = 0.014 [7, 195]), and 1999 (χ^2 = 5.55, df = 1, p = 0.018 [4, 207]) (shaded circles in Fig. 1*c*). The difference was marginally significant in 1996 (χ^2 = 3.75, df = 1, p = 0.05 [5, 179]). In all other years, there was no statistically significant difference between YOY-W densities from rainbow smelt invaded and uninvaded lakes (Mann–Whitney tests, all $p > 0.05$); however, statistical power to detect effects for any given year was low (mean number of invaded lakes for a given year = 5; mean number of uninvaded lakes for comparisons in a given year = 166).

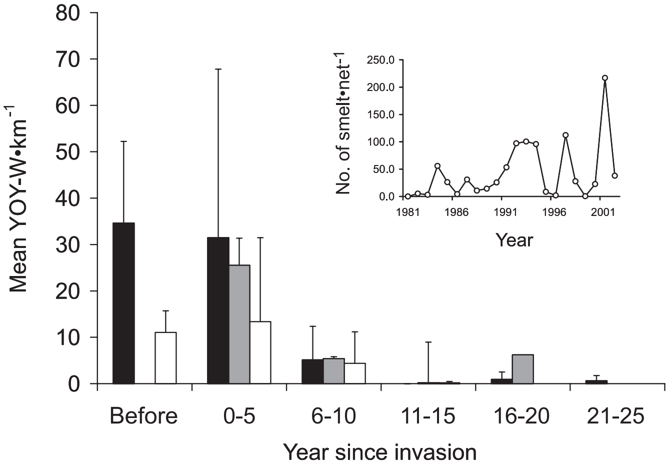
YOY-W density declined from pre- to post-invasion periods in the three lakes with pre- and post-invasion data (Fig. 2). Average YOY-W density in the first 5-year period after the first observation of rainbow smelt (31.47 YOY-W·(km of shoreline)$^{-1}$ remained similar to pre-invasion density (34.64) in Sparkling Lake, but declined in subsequent periods (5.12, 0.00, 0.92, and 0.64, respectively). Similarly, in Keyes Lake, average YOY-W densities in the first 5 years after rainbow smelt invaded (13.39 YOY-W·(km of shoreline)$^{-1}$ were similar to those before invasion (11.06), but declined thereafter (4.38 and 0.19). In Long Lake, average YOY-W densities were higher in the first 5 years after invasion (25.69 YOY-W·(km of shoreline)$^{-1}$ than in subsequent periods (5.12, 0.18, and 6.21, respectively). Densities of YOY-W decreased by an average 70% after rainbow smelt were found in Sparkling, Long, and Keyes lakes (90%, 70%, and 50%, respectively). Rainbow smelt abundance in Sparkling Lake increased rapidly following introduction, but also varied widely among years (Fig. 2, inset).

Fig. 1. (*a*) Trends (1985–2004) in young-of-the-year walleye (*Sander vitreus*) (YOY-W) densities (YOY-W·km^{-1}) in Wisconsin lakes with natural and stock-assisted recruitment. Mean annual YOY-W densities for uninvaded lakes with natural recruitment (A; open circles), stocked recruitment (B; solid circles), and both (C). (*b*) Mean annual YOY-W densities for rainbow smelt invaded (D; solid circles) and uninvaded (C; open circles) lakes. (*c*) Standardized YOY-W densities in invaded lakes; each point represents the difference between the mean YOY-W density for invaded versus uninvaded lakes for a year (Δ), divided by the standard deviation (SD) of the YOY-W density for uninvaded lakes (natural variation). Shaded points are YOY-W densities from invaded lakes significantly lower than those from uninvaded lakes (Mann–Whitney tests).



The effect of rainbow smelt on walleye recruitment was variable among invaded lakes. For the 10 invaded lakes with more than two YOY-W density estimates between 1985 and 2004, nine showed negative deviations from the mean YOY-W densities of uninvaded lakes (Fig. 3). The average deviation across all invaded lakes was –12.8% (range, +42% to –48%). Deviations were not related to any of the lake attributes that we ex-

Fig. 2. Mean young-of-the-year walleye (*Sander vitreus*) densities (YOY-W·km^{-1}) for three lakes in periods before and after rainbow smelt (*Osmerus mordax*) invasion: solid bars, Sparkling Lake; shaded bars, Long Lake; open bars, Keyes Lake. Five-year postinvasion periods are considered from the year in which rainbow smelt were first observed in each lake. Pre-invasion data include all estimations made prior to the first detection of rainbow smelt. Long and Keyes lakes did not have records in all periods. Long Lake pre-invasion records were not available; first density estimate was available a year after initial rainbow smelt detection. Inset: rainbow smelt (*Osmerus mordax*) fyke net catch rate in Sparkling Lake (Vilas County) in 1981–2003.



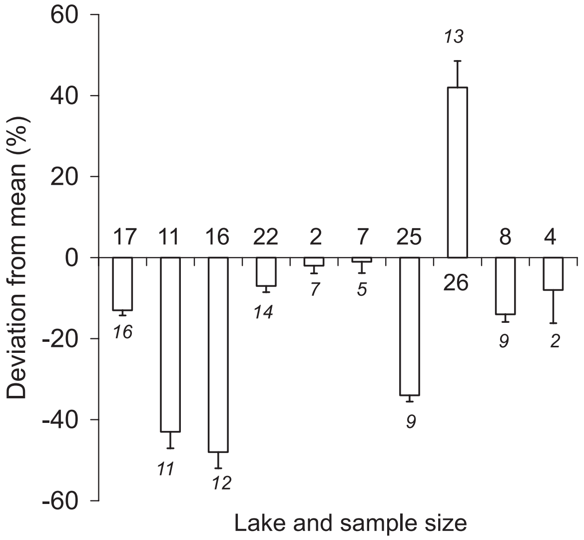
amined (maximum lake depth, $r^2 = 0.02$, $p = 0.66$; lake area, $r^2 = 0.012$, $p = 0.89$; average Secchi depth, $r^2 = 0.03$, $p = 0.63$; pH, $r^2 = 0.009$, $p = 0.93$).

Discussion

Invasions of exotic species are responsible for the decline of important fisheries in the Great Lakes region and elsewhere (Taylor et al. 1984; Franzin et al. 1994; Madenjian et al. 2000). Such effects, however, have often not become evident until it is too late to protect the remnant populations or reverse negative trends. When invasions are incipient, case studies are few and impacts are not easily detected. Regardless, it is critical to base management on the available (usually scarce) data derived from systems in which the invader has already had impacts and on existing biological and ecological information for species involved in the interactions.

The various approaches we used in our investigation indicate that walleye recruitment declines after rainbow smelt invasion of inland lakes in Wisconsin. We found lower recruitment in invaded relative to uninvaded lakes, as well as declines in recruitment over time following rainbow smelt invasion. Further evidence for the effects of rainbow smelt on walleye stems from the fact that all invaded lakes included in this study now require stocking to sustain walleye populations, whereas some were naturally reproducing populations in the past. Recruitment failure has also affected adult walleye abundance. In one of our study lakes (Sparkling Lake), Gilbert (2007) reported a decline in adult abundance from 1991 (6.0 walleye·acre^{-1}) to 1996 (2.6) and 2002 (2.1), with an abundance increase in 2006 (4.3) following extended-growth fish stocking efforts.

Fig. 3. Lake-specific deviations (%) (± standard error) in young-of-the-year walleye (*Sander vitreus*) densities for 10 rainbow smelt invaded lakes relative to uninvaded lakes. Each bar is labeled by the lake identification corresponding to lake number in Table 1. Smaller, italicized font is the sample size used in deviation calculations.



We have examined rainbow smelt impact on YOY-W densities because it is the most likely stage at which walleye populations could be affected. Adult walleye feed selectively on rainbow smelt, and in some instances, they have been used to aid in the recovery of native species that have been impacted by rainbow smelt. Krueger and Hrabik (2005) described how increases in adult walleye density via stocking and harvest restriction reduced rainbow smelt density and helped cisco recovery in three northern Wisconsin lakes. However, as YOY, walleye could be affected by rainbow smelt via competition or predation.

Rainbow smelt effects on walleye populations have been suggested in other systems. For example, Schneider and Leach (1977) reported a decline in walleye stocks throughout the Great Lakes in 1900–1940 and suggested that it could be partially due to an increase in rainbow smelt populations. Similarly, Jones et al. (1994) and Johnson and Goettl (1999) reported declines in YOY-W in Horsetooth Reservoir (Colorado, US) after introduction of rainbow smelt. Mechanisms for YOY-W density reductions were not identified in the aforementioned studies, but a reduction in zooplankton abundance and direct rainbow smelt predation of YOY-W were suggested. In addition to competitive and predatory relationships between rainbow smelt and walleye, we suggest that alteration of zooplankton communities (Beisner et al. 2003) and thiamine (vitamin B1) deficiency induced early mortality syndrome in YOY-W (Honeyfield et al. 2005; Tillitt et al. 2005) could be related to reduced YOY-W densities in rainbow smelt invaded lakes. Research conducted on Sparkling Lake (an invaded lake in this study) in the summer of 2006 will directly assess the interactions between rainbow smelt and walleye (T. Ahrenstorff and G. Sass, unpublished data). At present, the abundance and sex composition of mature walleye stocked into Sparkling Lake should result in the production of naturally reproduced offspring. The goal of this study is to extensively monitor the fate of any naturally reproduced walleye in Sparkling Lake. To ensure that information is collected on rainbow smelt – walleye interactions given the uncertainty in natural reproduction, 2 million OTC-marked walleye fry will also be stocked into Sparkling Lake by the WDNR to examine the contribution of stocked versus naturally reproduced walleye (S. Gilbert, personal observation).

We have based our estimation of rainbow smelt impact on walleye on one of the most variable processes in population and fisheries biology: recruitment. The high variability of recruitment among walleye populations and the variety of factors that influence this process pose challenges to the detection of rainbow smelt effects. However, the strong declines observed in Wisconsin lakes, also supported by evidence from other systems, indicate that rainbow smelt introductions can be major drivers of walleye population dynamics. Our study was based on a relatively small number of invaded lakes, which led to low statistical power to detect effects. Rather than a limitation, we consider this current lack of invaded systems to be an opportunity to call attention to the potential threat of rainbow smelt invasion on walleye populations.

The magnitude of rainbow smelt impact on YOY-W densities varied among lakes, and we were unable to find a relationship between lake-specific attributes and the extent of the decline. Although this may again be a product of the small number of lakes available for analysis, we suggest that other factors such as lake-specific walleye stocking histories, shoreline development factors, rainbow smelt habitat availability, rainbow smelt and walleye predator–prey interactions, and the extent of thiamine deficiencies in walleye due to rainbow smelt predation could be explored in future efforts to explain this variability.

Alternative hypotheses that could lead to our results are unlikely. However, it is possible that rainbow smelt are more likely to invade lakes that support poor walleye populations, which would presumably have lower YOY-W densities. Although this is possible, results for the three lakes with long-term data indicate adequate walleye recruitment prior to rainbow smelt detection. Additionally, factors that decrease walleye abundances periodically, such as natural recruitment variability and angler harvest, may allow any lake with a walleye population and adequate rainbow smelt habitat to be susceptible to rainbow smelt invasion effects.

A large number of walleye populations in the Great Lakes region could be affected by rainbow smelt invasions (Mercado-Silva et al. 2006). Although rainbow smelt invasion may not lead to a decline in walleye recruitment in every lake, our results indicate that impacts on walleye are likely and the large number of vulnerable lakes should prompt efforts to prevent further invasions. In addition, walleye populations are subject to increasing angling pressure. In northern Wisconsin, the human population increased by about 60% between 1970 and 2000 (BIA 2003) and continues to grow. The depletion of walleye recruitment as a consequence of these joint pressures should be taken into account when establishing future walleye fishery regulations.

Stocking has been the preferred strategy for walleye population management in Wisconsin since the 1870s but has had relatively low overall success, with ~85% of fry stockings resulting in no measurable year class (Bureau of Fisheries Management (BFM) 1999). Walleye recruitment declines associated with rainbow smelt invasion are likely to increase walleye stocking costs. Because walleye fry are affected by rainbow smelt predation, stocking walleye fingerlings (~50 mm total length) and extended-growth fingerlings (>130 mm total length) may be alternatives to support walleye populations. Although stocking fingerlings is more expensive than stocking fry (Loadman et al. 1986; BFM 1999), the potential increased survivorship of larger individuals may offset these costs and augment walleye populations more effectively.

Current efforts to prevent rainbow smelt invasion include enhancing awareness of the impact of invasive species. However, further efforts are required to prevent their impact on walleye. Given our results, invasive species effects should be added to the 30 key issues that have been identified by the Wisconsin DNR Walleye Management Planning Committee (Hewett and Simonson 1998) as those that need to be addressed for the future management of walleye populations in the state.

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